Notes on the Life Cycle and Natural History of Butterflies of El Salvador. III B.—*Hamadryas amphinome* L. (Nymphalidae-Hamadryadinae)

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Abstract: The complete life cycle of *Hamadryas amphinome* L. is presented in this article with photographic illustrations, with a record of the foodplant exploited by the larvae in El Salvador, *Dalechampia scandens* L., and an account of the larval and adult behavior. This species apparently is the most evolved of the *Hamadryas* complex as evidenced by the notable deviations from the behavior of the other species studied: *H. februa* and *H. guatemalena*, which are solitary during all phases of the metamorphosis, and *H. amphinome*, which is gregarious in the larval stage and shows consistent group behavior of the adults. Emphasis is made of the behavioral adaptations the different species of the genus have gone through which gradually change from fully solitary to fully gregarious larval habits.

This is the third article of a series on butterflies of the Hamadryadinae group of the Nymphalidae, presenting our observations on the developmental time and behavior of the early stages and the adults of *Hamadryas amphinome* L. The field studies were conducted in the area of Los Chorros (a tourist resort, about 12 km W of San Salvador, capital city of El Salvador), where the species is fairly abundant throughout the year. During the dry season 1972/73 (November through April), a group of second instar *Hamadryas* larvae were found feeding on *Dalechampia scandens* L., which were different from those of *H. februa* and *H. guatemalena*. It was a surprise to us to notice that these larvae, unlike the others just mentioned, which have solitary behavior, were feeding in a tight group on the underside of the leaf, showing thus gregarious habits. The resulting adults were *H. amphinome*. Searches for eggs were made every weekend from that time with negative results until 26 August 1973, when one peculiar group of "strings" formed by eggs one on top of the other was found and collected. These were reared and the adults emerged about one month later. Since then the species has been reared several times up to this date. The rearing of the larvae in our insectarium was in transparent plastic bags, sealed with rubber bands, in which fresh leaves of the foodplant were supplied every third day until pupation of the larvae.

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Some colonies were kept together during the whole larval stage; others were split in half after every moult starting from the second instar, so as to end up with 4 to 6 individuals per bag. When ready to pupate the larvae were transferred to a wooden box with windows of mosquito-netting and kept there until the adults emerged. Records were kept of the developmental time and size of each instar; photos were taken of all phases of the metamorphosis; and specimens of eggs, larvae in the different instars and of the pupae have been preserved in alcohol to be sent to the American Museum of Natural History, New York.

LIFE CYCLE STAGES

Egg. About 1 mm in diameter, round with slightly flattened base, yellowish-white when recently deposited, turning to gray when ready to hatch. Surface almost smooth except for faint sculpturing on the upper part of the walls. Eggs in groups of strings of eggs one on top of the other, totalling 30 to more than 100 eggs per group. Hatch in 4–5 days.

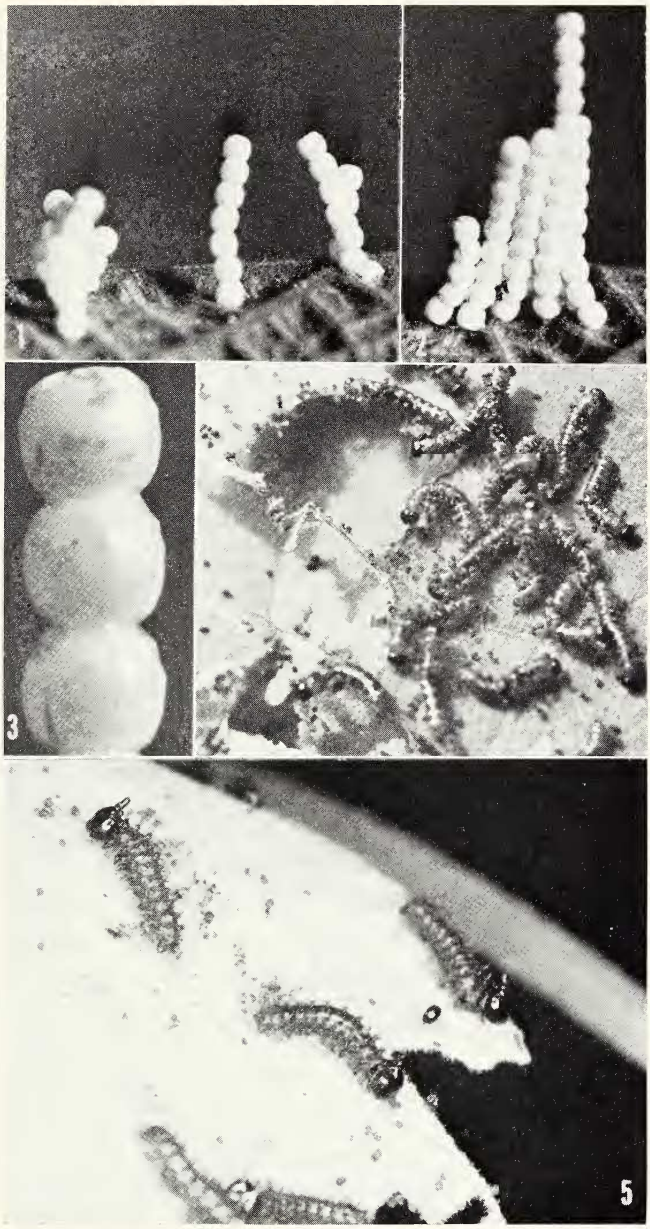
First instar larva. Head shiny black, slightly cordiform, naked. Body whitish before feeding, turning to olive green, with transverse rows of dark setae. Grows to 4 mm in 2–3 days.

Second instar larva. Head shiny black with short horns on apices of epicrania. Body brownish-green with transverse rows of short furcate spines. Grows to 8 mm in 2–3 days.

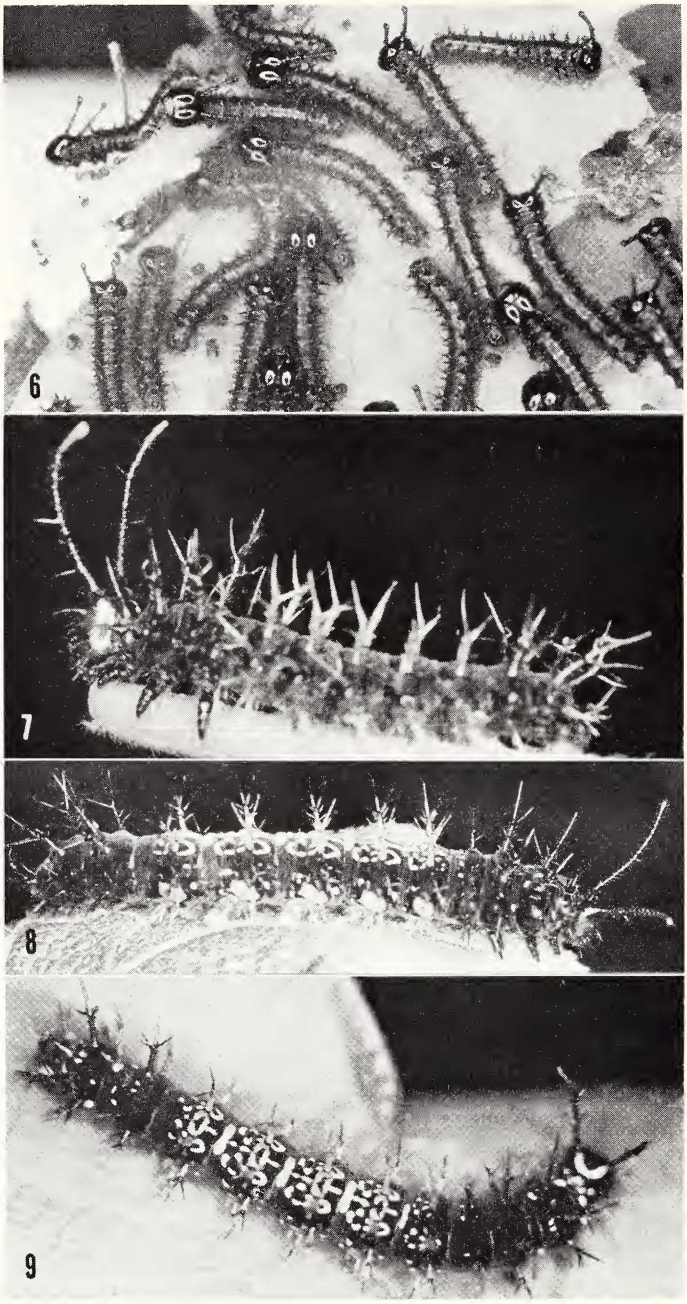
Third instar larva. Head shiny black with two lateral spines and long slender horns on apices of epicrania each terminating in a clubbed tip. The shafts of the horns are armed basally with one secondary spine directed anterad, a little higher a second spine directed slightly inwards, then higher a third directed outwards, still higher a fourth parallel to the first and finally, about the middle of the shaft, a fifth spine parallel to the second. The rest of the shaft is covered by sparse short setae. Body dark greenish-brown with short furcate spines placed in the following order: on first thoracic segment (T-1) one subdorsal bifurcate spine, one supraspiracular bifurcate spine and one subspiracular simple spine; T-2 with one 5-furcate subdorsal spine, one 5-furcate supraspiracular spine sided by a simple spine, one subspiracular simple spine sided by another very small simple spine; T-3 with one prominent 6-furcate subdorsal spine, one 4-furcate supraspiracular spine sided by a simple spine, and one subspiracular simple spine sided by another small one. First abdominal segment (A-1) with one 4-furcate subdorsal spine, one small supraspiracular simple spine, one bifurcate subspiracular spine, one supraventral simple spine in line with the legs. From A-2 to A-6, one 4-furcate subdorsal spine, one 4-furcate supraspiracular spine, one 3-furcate subspiracular spine sided by a simple spine, and two supraventral simple spines. Segments A-7 and A-8 show in addition one 5-furcate dorsal spine. Segment A-9 has only one 6-furcate supraspiracular spine deflected posterad. A-10 has an anal plate with a crown of 4 small simple spines. Grows to 1.2 cm in 2–3 days.

Fourth instar larva. As in third instar, but the head is orange-red, has longer lateral spines and longer horns, which are incurved slightly caudad. Body spines longer than in third instar, the subdorsal ones on segments A-2 to A-6 taking an orangish tinge. Grows to 2.6 cm in 4–6 days.

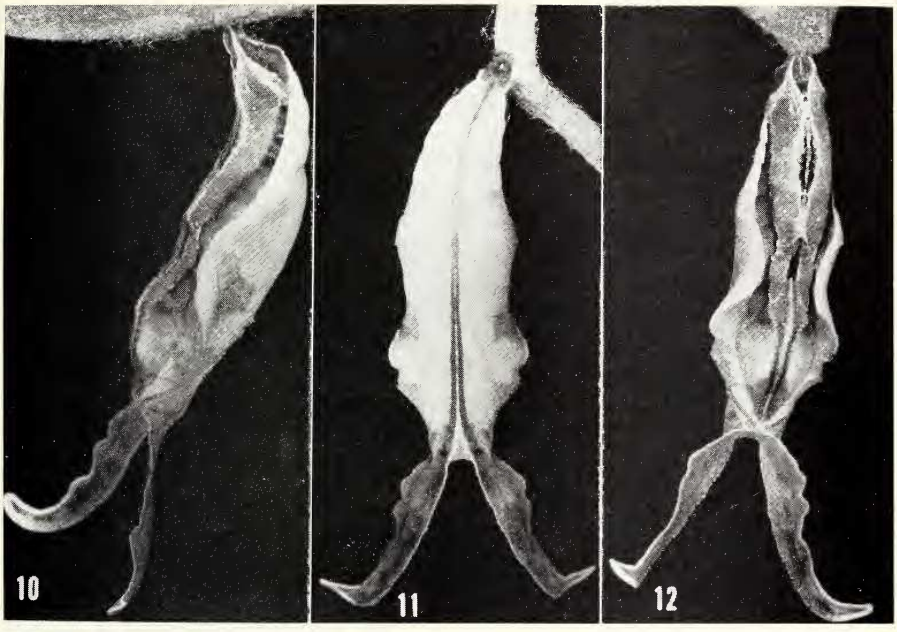
Fifth instar larva. Main change is body color, which is black; from A-2 to A-6 bright yellow dorsal design of circles and bars forming paired O T O s. Subspiracularly these



Figs. 1–5. *Hamadryas amphinome* L. 1 and 2. Typical ovipositions of *Hamadryas amphinome* in groups of strings. Note that they are upside down, the strings being actually pendant from the lower surface of the leaves. 3. Close-up of eggs. 4. Group of first instar larvae ready to moult. 5. Group of second instar larvae. The rest had dropped to the ground when disturbed while taking the photo. Notice the reflection of the ring-flash on the shiny head capsule.



FIGS. 6–9. *Hamadryas amphinome* L. 6. Group of third instar larvae. Ovals on head are the ring-flash reflections. 7. Fourth instar larva. 8 and 9. Lateral and dorsal view of fifth instar larva where subspiracular orange spots and paired O T O marks are clearly visible.



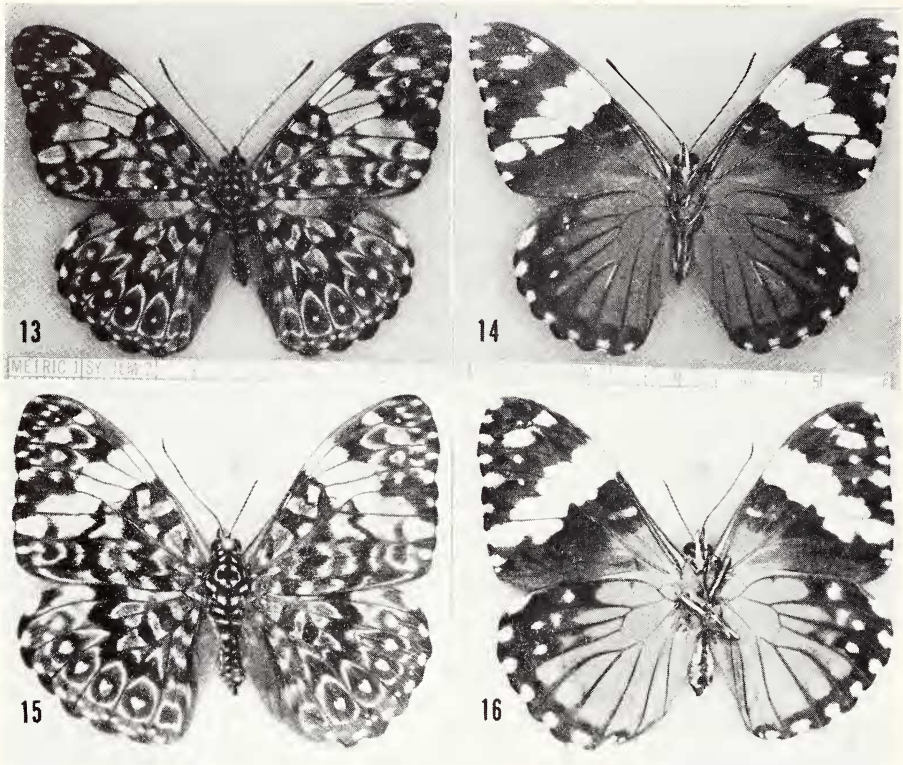
Figs. 10–12. *Hamadryas amphinome* L. 10. Pupa, lateral view. 11. Pupa, ventral view. 12. Pupa, dorsal view.

segments show a large bright orange spot which contributes to make the larva very conspicuous. The spines on these segments are also reddish-orange. The subdorsal spines on T-2 and T-3, and to a lesser degree the ones on A-2, A-7 and A-8, as well as the dorsal spines on the last two, present small secondary spines on the shaft of the scoli. Grows to 4.5–4.7 cm in 5–6 days.

Pre-pupa. No change in coloration. It is slightly shorter. Hangs with head and thorax incurved ventrally for one day.

Pupa. Thickens abruptly from flat cremaster, then gradually to A-2 and A-3, narrowing then dorsally and laterally to A-1, thickening again to T-2, narrowing finally towards the head, which is provided with two long, flattened and incurved prolongations. The prolongations are diverging laterally and incurved outwards at the tips. Usual color dorsally light brown with green bordering along wingcases and on thoracic segments; darker brown, bordered by very light brown lines along abdominal meson. Ventrally light green, except cremaster and head prolongations, which are brown. There is a darker morph on which the green is substituted by light brown, the rest being darker brown than usual. It looks very much like a rolled decaying leaf. Measures up to 4.5 cm long (including head prolongations) and lasts 7–8 days.

Adults. No marked sexual dimorphism in this species, the females having front wings larger than males. Ground color dorsally black with many dark blue squares, half-moons, round spots and bars forming a complicated pattern, covering both front and hindwings, except for a subapical row of elongated light gray spots running from mid-costal margin to tornus of front wing. The blue color of both wings is highly re-



FIGS. 13–16. *Hamadryas amphinome* L. 13 and 14. Male, dorsal and ventral view. 15 and 16. Female, dorsal and ventral view.

flectant. Front wing ventrally mostly dull black with orange basal triangle, and a subapical reproduction of the dorsal gray spots in light yellow. Hindwing mostly bright orange with a black area along the outer margin, which shows a row of cream colored round spots. Body dorsally matching the black and blue colors of the wings, ventrally thorax orange and abdomen black with two longitudinal cream stripes. Antennae and proboscis black. Wing span varies from 6 to 7 cm. Total development in captivity takes from 27 to 35 days. The colonies kept together during the entire larval stage do not develop as big a larva as the ones split gradually into smaller groups from the second instar on, consequently the adults from the large groups are also much smaller than normal, even though the time elapsed is about the same.

NATURAL HISTORY

The foodplant of *Hamadryas amphinome* in El Salvador is the same foodplant used by *H. februa* and *H. guatemalena: Dalechampia scandens* L., a vine belonging to the Euphorbiaceae, which we mentioned in detail in previous articles on other *Hamadryas* spp. (Muyshondt & Muyshondt 1975 a and b). It is to be noted that *H. amphinome* appears to have a more restricted range

than the species mentioned before, which are found within the whole range of the foodplant (500 to 1500 m altitude). *H. amphinome* is rather common around 1000 m altitude, always in the close neighborhood of wooded land surrounded by pastures or low-brushy plant communities.

The females of *H. amphinome* oviposit on the undersides of leaves of medium development of *D. scandens*, from about two meters to very close to the ground. The females perform outstanding acrobatics while depositing the strings of eggs, spending close to 45 minutes to deposit some 50 eggs. The eggs are laid one by one, one below another, forming perfect pendant strings. There is no consistent norm of the number of eggs per string. We have found groups of eggs with strings from 1 to 13 eggs. Müller (1886) records two groups containing strings from 10 to 15 and from 2 to 13. In our experience most of the strings consist of 5 to 10 eggs. The range of eggs per oviposition is from 30 to more than 100, but most of the groups average 40 to 50 eggs. The strings are rather rigid and keep the same angle in relation to the leaf surface, even if the leaf is turned upside down, contrary to what Müller (1886) observed about *Ageronia* (= *Hamadryas*) *fornax* Hübner, whose eggs are deposited in one single flexible string which always hangs perpendicular to the ground. The eggs of *H. amphinome*, white or cream-white when recently deposited, turn to dark gray before hatching.

The hatching larvae eat their way out from the lateral wall of the eggshell which is an important adaptation acquired by the species to avoid damaging an adjacent egg and also prevents the rest of the eggs from falling to the ground, which would occur if the exit hole was eaten from the micropylar area as is customary in many other species. The small larvae have to crawl up the string to reach the leaf surface and there the group is formed. They start eating the lower layer of leaf tissue. Their excrements adhere to the thin layer of silk formed while the larvae weave a silken foothold as they move about. The small larvae also affix some pellets to their bodies. The resultant accumulation of excreta seems to be a protective device adopted by this species against its enemies. Later, but still during the first instar, the larvae move in a group to the edge of the leaf, and form a tight line of individuals perpendicular to the edge. As the larvae grow in the subsequent moults, the group starts segregating into smaller groups mainly due to space limitations of the leaf, somewhat similar to what happens with *Dione juno huascama* Reakirt (Muyshondt, Young and Muyshondt, 1973), but also due to the habit of *H. amphinome* larvae of wiggling convulsively at the least disturbance, which if continued provokes a massive dropping of the larvae from the leaf to lower levels of the plant or to the ground. In the act of crawling back to the plant and reforming the group some larvae end up forming smaller communities, far from each other. By the end of the larval stage, the groups are usually reduced to three to seven individuals. When

ready to pupate the small groups dissolve and the larvae wander about the plant independently until a suitable location is chosen. This is normally on the same vine or on a supporting plant, among the thick foliage, where the larvae weave a silken mat and after cleaning their digestive tract, hang from their anal prolegs, with head and thorax incurved ventrally, until pupation. We have never found groups of pupae in the fields. The pupae of *H. amphinome*, except for the head prolongations and the body color, look very much like the pupae of *H. februa* and *guatemalena*, and behave very much like them, swinging violently from side to side at the faintest provocation, ending bent to one side. The vertical position is resumed some time afterwards. As with the other species mentioned, the pupae are firmly anchored on the flat cremaster so that they keep vertical to the supporting object even when this is turned upside-down.

The emerging adults hang from the pupashell while ejecting the reddish meconium and expanding the wings, which are held folded dorsally. After the first flight the wings are usually kept spread open, except for night resting. Even then at the slightest movement of the plant, the wings are immediately spread, but after some flappings are folded again. The adults are seen, at times, flying rapidly one following another in groups from five to eight individuals, as if playing "follow-the-leader." When so acting, they alight, eventually, separately on contiguous fence poles or trees. When one flies again, the whole group follows and after some fast maneuvers, the group alights again on the same places or close by. This apparent game has been observed for considerable periods of time, until the group moves away. When in this playful mood, no "clicking" has been noticed. At other times, when two males encounter each other, frantic circumvolations and excited clicking do occur. Sometimes the fighting males fly up vertically, while circling, more than 100 meters high, coming down vertically also. One of us (A.M., Jr.), timed one such a fight, and it lasted about 45 minutes, while continuous clicking was audible. Females ready to oviposit fly more slowly than usual until they locate a foodplant, and land on the underside of a medium sized leaf. They stay there for a long period of time until a considerable number of eggs are deposited as described, moving away afterwards with their customary swift flight. In both males and females the blue reflection seems to hover over the flying adults, somewhat as in the blue Morphos. In all other respects the adults of this species behave like the rest of the *Hamadryas* group, and it would be repetitious to further describe their habits. The species is also subject to heavy parasitism by tachinid flies.

DISCUSSION

W. Müller (1886) describes, briefly, the life cycle of *Hamadryas* (= *Ageronia*) *amphinome* and gives the time spent during the larval stage as 19 to

22 days, not determining the pupal time. He gives for the egg period 3 days, which in our experience has taken from 4 to 5 days. The times for the different instars of the larva are more in accordance with our findings, which makes us believe he found the eggs a day or two after they were deposited. Müller does not mention the foodplant when dealing with *H. amphinome*, but when he treats the genus *Ageronia* Hübner, he states that all the species included therein, feed, in Brazil, on *Dalechampia* (*triphyla* Lam., *ficifolia* Lam., *stipulacea* Müll. Arg.), which agrees with our findings. Young (1974) records *Dalechampia heteromorpha* as the foodplant of *H. februa* in Costa Rica. Amazingly Barcant (1970) mentions *Aristolochia trilobata* (an Aristolochiaceae) as the foodplant of *H. amphinome*! In El Salvador where Aristolochiaceae are well represented by several species, we have never found any *Hamadryas* on them. Aristolochiaceae seem to be exploited in El Salvador exclusively by various species of *Battus* and *Parides* (Papilionidae). Most probably Barcant's record is a case of plant misidentification. The present is apparently the first complete life cycle description of *H. amphinome*, with photographic illustrations, ever published.

Hamadryas amphinome, which is the type species of the genus *Hamadryas* Hübner, teste Hemming (1967), is of extreme interest to specialists in evolution studies as it seems to be the most advanced species of the *Hamadryas* complex. This is evidenced by the gradual changes in various aspects of the behavior of the various species, and in the shape of the eggs. *H. arete* Doubleday deposits one very sculptured egg at a time (Müller, 1886), and the larva is solitary. *H. februa* Hübner and *H. guatemalena* Bates (Young, 1974; Muyshondt & Muyshondt 1975 a and b), usually deposit their sculptured eggs individually, the larvae then being solitary also, but these two species might deposit two or even three eggs one on top of the other, the resulting larvae then leading a loose communal life. All these species share the peculiar perch-making habit during the first larval instars. *H. fornax* (Müller, 1886) deposits the sculptured eggs in one string containing up to 10 eggs at a time (one egg on top of the other), and the ensuing larvae have gregarious habits. Finally *H. amphinome* deposits its almost round, little sculptured eggs in groups of several strings totalling at times more than 100 eggs per group, and the larvae also are gregarious. The last two species have abandoned the perch-making habit. In *H. amphinome* even the adults seem to maintain a sort of loose gregariousness, as their "follow-the-leader" game seems to indicate.

The shift from solitary to gregarious behavior of the *Hamadryas* complex, taken as a whole, has produced the following remarkable deviations from the probable original solitary behavior: 1) the egg laying technique, which has affected the shape of the eggs, 2) prerequisite to the massive egg laying, the larvae must have acquired the habit of eating the exit hole from the side of

the eggshell instead of the micropylar area, a trait existent already in the solitary species. 3) The abandonment of the perch-making habit, shown by the solitary species, in favor of the frass-pellet sticking on the underside of the leaves. 4) the angry disposition of the gregarious species, contrasting with the rather passive attitude of the solitary species. 5) The gradual increase in gaudiness of the larval coloration in the gregarious species, as compared to the solitary ones, and 6) the ability to produce disagreeable scent, enhanced by the number of individuals in close association exhibited by the gregarious species.

It is probable that the acquisition of the gregarious larval behavior is a relatively recent event, as apparently the species is not yet fully adapted to some of its consequences (ochlesis), as would be suggested by the readiness of the groups to part company at the faintest motivation, as if to avoid overcrowding of individuals. Overcrowding in captivity, has led to a drastic reduction in the size of the adults. In other gregarious species of butterflies we have observed (*Actinote* spp., *Phyciodes* spp., *Chlosyne* spp., *Thessalia theona* Ménétries, *Microtia elva* Bates, *Mechanitis isthmia* Bates, *Colobura dirce* L. *Manataria maculata* Hopff.) there seems to be a better adaptation to the crowding resulting from the communal life, and the individuals only disperse just prior to pupation. In one case (*Dione juno huascama* Reakirt) we have even found communal pupation in the fields (Muyshondt, Young and Muyshondt, 1973). If in these species there is a certain amount of segregation of the original group into smaller ones, it is mostly due to space limitation. It is true that these species, if deprived of sufficient food and space to move about, do also produce midget adults, but not when they have enough food and ample space. We emphasize also the contrast between the angry convulsions of the larvae of *H. amphinome* with the coordinated twitchings of a mass of *Dione juno huascama*. All these factors indicate that most of the gregarious species acquired such behavior much longer ago than *Hamadryas amphinome*, and are better adapted to it.

It seems to us that the conspicuous larval coloration of *H. amphinome*, added to the unpleasant odor emitted by the larvae, the adults' aggressive disposition and the bright orange coloration of their underwings, suggest impalatability to predators (orange color in insects is usually associated with such condition), even though there is still some crypsis in the dorsal coloration of the wings. The urticant properties of the foodplant *Dalechampia scandens*, which belong to the Euphorbiaceae family reputed to comprise plants with caustic or otherwise poisonous constituents (Standley, 1923, says about Euphorbiaceae: "The sap usually has purgative and often poisonous properties"), would seem to sustain our assumption, even though Young (1974) has observed, in relation to *Dalechampia heteromorpha* Pax and Hoffmann, which

is one of the foodplants of *H. februa* in Costa Rica: "I chewed several leaves (both young and old) and found no signs of bitter tastes." In our experience some alkaloid (supposedly poisonous) bearing plants are not bitter when chewed, and on the other hand some which are bitter when chewed do not contain alkaloids. Furthermore, alkaloids are not the only poisonous materials found in plants: saponins, cyanogenetic and cardiac glycosides are others (Brower & Brower, 1964), and are not necessarily associated with bitter tastes.

H. amphinome, as is the case with *H. guatemalena* (Muyshondt & Muyshondt, 1975 b) has lost all the dorsal spines with the exception of the one on segments A-7 and A-8, which are present on all abdominal segments (except the A-9 and A-10) of other species of *Hamadryas*, probably as a result of the increased protection obtained from the more efficient exploitation of the noxious components of the foodplant, enhanced in this case by the gregarious behavior of the larvae.

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